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Patterns of fMRI Activity Dissociate Overlapping Functional Brain Areas that Respond to Biological Motion

Report

Marius V. Peelen,[1,*] Alison J. Wiggett,[1] and Paul E. Downing[1,*]

[1] School of Psychology
University of Wales
Bangor, Gwynedd LL57 2AS
United Kingdom

Summary

Accurate perception of the actions and intentions of other people is essential for successful interactions in a social environment. Several cortical areas that support this process respond selectively in fMRI to static and dynamic displays of human bodies and faces. Here we apply pattern-analysis techniques to arrive at a new understanding of the neural response to biological motion. Functionally defined body-, face-, and motion-selective visual areas all responded significantly to "point-light" human motion. Strikingly, however, only body selectivity was correlated, on a voxel-by-voxel basis, with biological motion selectivity. We conclude that (1) biological motion, through the process of structure-from-motion, engages areas involved in the analysis of the static human form; (2) body-selective regions in posterior fusiform gyrus and posterior inferior temporal sulcus overlap with, but are distinct from, face- and motion-selective regions; (3) the interpretation of region-of-interest findings may be substantially altered when multiple patterns of selectivity are considered.

Introduction

One of the most important functions of vision is to provide information about the actions, intentions, and identities of other individuals. Functional magnetic resonance imaging (fMRI) research into how the human visual cortex accomplishes this task has identified neural activity in a number of posterior areas that are selective for the visual appearance of conspecifics. In the human, the extrastriate body area (EBA; Downing et al., 2001), which is found at the posterior end of the inferior temporal sulcus (partly overlapping motion-selective area hMT+), is selective for static images of human bodies and body parts. Face-selective responses are found in posterior fusiform gyrus, particularly in the right hemisphere (fusiform face area, or FFA; Kanwisher et al., 1997). More recently, strongly body-selective responses have also been reported in the posterior fusiform gyrus, in a region closely overlapping the FFA: the "fusiform body area," or FBA (Peelen and Downing, 2005a; Schwarzlose et al., 2005). Finally, realistic and schematic biological movements of the hands, face, and whole body reliably activate posterior superior temporal sulcus (pSTS; Allison et al., 2000; Beauchamp et al., 2002; Bonda et al., 1996; Haxby et al., 2002; Pelphrey et al., 2005).

A major focus in the neuroimaging research on biological motion processing has been on selective neural responses to "point-light" (PL) animations (Grèzes et al., 2001; Grossman et al., 2000, 2004; Grossman and Blake, 2001, 2002; Michels et al., 2005; Peuskens et al., 2005; Santi et al., 2003; Saygin et al., 2004; Vaina et al., 2001). These displays, originally conceived by Johansson (1973), consist of only a few dots that move in a way characteristic of human movements, e.g., walking or jumping. They are of theoretical interest because they convey biological motion patterns with little or no form information in individual frames and without most of the visual features (e.g., clothes, skin) normally present in images of moving human bodies. Interpretation of fMRI studies comparing PL figures to various controls has largely focused on pSTS. But biological motion consistently activates other posterior regions, even when low-level factors such as the presence of visual motion per se are accounted for. To date, the presence of these activations and their functional significance remain unexplained.

Several studies have reported activations to PL action animations in fusiform gyrus (Grossman and Blake, 2002; Grossman et al., 2004; Santi et al., 2003). Grossman et al. (2004) have interpreted this finding as reflecting engagement of face-selective FFA by PL animations. However, given its close proximity, this activation could instead (or additionally) reflect activation of body-selective FBA. PL figures also activate the posterior inferior temporal sulcus/middle temporal gyrus (Michels et al., 2005; Peuskens et al., 2005; Saygin et al., 2004). It is at present unclear whether this activation reflects activation of body-selective neurons in the EBA (compare Downing et al., 2001, and Michels et al., 2005, with Grossman and Blake, 2002) or, instead, motion-selective neurons in area hMT+.

Here we provide a simplifying resolution to these open questions by demonstrating that PL-related responses outside of pSTS reflect engagement of known neural regions that are selective for static images of the human body. By performing voxel-by-voxel analyses of the response patterns to different stimuli, we were able to disentangle body-selective from face- and motion-selective responses in posterior fusiform gyrus and inferior temporal sulcus. In all regions tested, body selectivity, but not face or motion selectivity, could predict the response to biological motion displays on a voxel-by-voxel basis.

Results

Our experimental approach was as follows. First, we used a whole-brain, group-average analysis in order to identify gross regions that respond more to human actions, rendered as point-light animations, than to scrambled controls. Second, we identified several functional ROIs: hMT+, EBA, FFA, and FBA. We then measured the response of these individually defined ROIs to the biological motion stimuli. Finally, we performed a series of

*Correspondence: pspe40@bangor.ac.uk (M.V.P.); p.downing@bangor.ac.uk (P.E.D.)

voxel-by-voxel pattern analyses (Cox and Savoy, 2003; Haxby et al., 2001; Haynes and Rees, 2005; Kamitani and Tong, 2005) on individually defined ROIs, with the goal of discovering the relationship between biological motion selectivity and motion, face, and body selectivity in those regions.

Eighteen subjects were tested on three blocked-design experiments. In the main experiment, point-light renderings of simple whole-body actions were compared to scrambled versions of the same sequences. As in a previous study (Grossman et al., 2000), the scrambled condition was created by randomizing the starting points of the light points from the intact sequences, but keeping the motion patterns intact. The other two experiments were used to identify functional regions of interest in each subject. One compared oscillating to static low-contrast rings in order to identify hMT+. The other experiment compared the responses to bodies (without heads), faces, scenes, and tools in order to localize the body-selective regions EBA and FBA and face-selective FFA.

Whole-Brain Analysis

An initial whole-brain group-average contrast between the point-light biological motion display and the scrambled control motion display revealed activation in various visual areas (Table 1). Replicating previous studies, strong activation was found in right posterior superior temporal sulcus (pSTS). We also found significant activation in bilateral posterior inferior temporal sulcus (pITS) and posterior fusiform gyrus (pFG). The peak coordinates of the pITS activation were close to those typical both for the EBA (Downing et al., 2001; Peelen and Downing, 2005b) and for hMT+ (Dumoulin et al., 2000). The right fusiform activation fell close to the typical coordinates of the FFA and the FBA (Kanwisher et al., 1997; Peelen and Downing, 2005a). Thus, the group-average analysis confirms the existence of significant biological motion selectivity in pITS and in pFG. The aim of the following analyses was to examine this selectivity in closer detail, on an individual subject level, in order to determine its source.

Regions of Interest

The EBA, hMT+, FBA, and FFA were localized in each subject individually. The mean sizes of the ROIs were (mm^3 [SD]): left EBA (586 [146]), right EBA (605 [114]), left hMT+ (595 [97]), right hMT+ (554 [168]), right FBA (193 [145]), right FFA (323 [167]). Average peak Talairach and Tournoux (1988) coordinates for the EBA and hMT+ were (x [SD], y [SD], z [SD]): left EBA (−45 [5], −74 [4], −1[8]), right EBA (48 [5], −70 [5], 1 [6]), left hMT+ (−44 [5], −68 [4], −4 [8]), right hMT+ (44 [4], −66 [6], −2 [7]). Average peak Talairach coordinates for the individually localized right hemisphere FBA and right FFA were: FBA (41 [3], −45 [7], −19 [5]), FFA (39 [4], −47 [7], −19 [4]). Note that the average coordinates of EBA and hMT+ (within each hemisphere) were very similar and that both were equally close to the pITS activation to biological motion in the group average analysis (left: −42, −70, −4; right: 44, −69, −7). Furthermore, even within single subjects, EBA and hMT+ overlapped substantially (Figure 1A). Likewise, the average coordinates of FBA and FFA were similar to each other and were similar to the group average biological motion fusiform gyrus activation (36, −39, −19). These regions also overlapped substantially within subjects (Figure 1B).

Table 1. Group-Average Activation for the Biological Motion Display

Region	Talairach Coordinates X	Y	Z	Mean T	mm^3
R. ITS	44	−69	−7	4.63	2101
R. ITS	52	−51	3	4.49	920
R. STS	57	−41	21	4.17	112
R. Fusiform	36	−39	−19	4.72	748
R. Fusiform	34	−68	−18	4.32	174
R. Post. Occipital	14	−96	−4	4.43	151
L. ITS	−42	−70	−4	4.59	2544
L. Supramarginal	−56	−39	25	4.37	388

Group-average activations for which biological motion was greater than scrambled motion, from a random-effects multiple-regression analysis, thresholded at $p < 0.001$ (uncorrected for multiple comparisons) and a minimum cluster size of 100 mm^3. Each row gives the anatomical location of the activation, the Talairach coordinates of the peak voxel, the mean T value, and the volume of activation. ITS, inferior temporal sulcus; STS, superior temporal sulcus.

In each of the individually defined ROIs, we extracted the magnitude of the response to the two conditions in the biological motion experiment and tested the difference between these conditions using repeated-measures ANOVAs and t tests.

Figure 2A shows the activation in left and right EBA and hMT+ for the two conditions in the biological motion experiment. A three-way repeated-measures ANOVA (hemisphere × ROI × condition) revealed no significant interactions with hemisphere. ROI interacted significantly with condition ($F_{1,17} = 16.6$, $p < 0.001$), indicating a stronger effect of biological motion in EBA compared to hMT+. Paired-sample t tests, however, showed that in each individual region the effect of biological motion was highly significant (left EBA: $t_{17} = 6.5$, $p < 0.001$; right EBA: $t_{17} = 5.3$, $p < 0.001$; left hMT+: $t_{17} = 4.2$, $p < 0.001$; right hMT+: $t_{17} = 5.3$, $p < 0.001$). Notably, a significant effect of biological motion was also found when the biological motion effect was measured from only the single most-selective (peak) voxel of each individual's ROIs (left EBA: $t_{17} = 7.3$, $p < 0.001$; right EBA: $t_{17} = 5.1$, $p < 0.001$; left hMT+: $t_{17} = 4.5$, $p < 0.001$; right hMT+: $t_{17} = 3.0$, $p < 0.01$).

Figure 2B shows the analogous results from right FBA and FFA. A two-way repeated-measures ANOVA (ROI × condition) showed a significant interaction between ROI and condition ($F_{1,17} = 6.0$, $p < 0.05$), indicating a stronger effect of biological motion in FBA compared to FFA. Paired-sample t tests showed that in both regions the effect of biological motion was significant (FBA: $t_{17} = 4.2$, $p < 0.001$; FFA: $t_{17} = 2.6$, $p < 0.05$). A significant effect of biological motion was also found when each ROI was defined by only the most selective voxel (FBA: $t_{17} = 3.4$, $p < 0.005$; FFA: $t_{17} = 3.2$, $p < 0.01$).

Interim Summary

Thus, left and right EBA, left and right hMT+, right FBA, and right FFA all show a strongly selective response to biological motion animations. This holds true whether the ROIs are defined as clusters of significant voxels

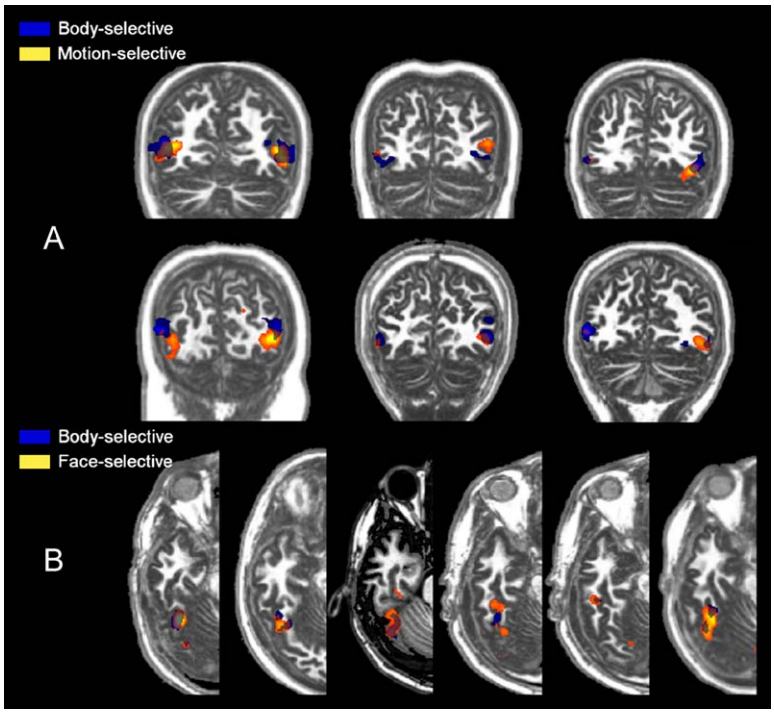

Figure 1. Overlap of Nearby Brain Areas in Individual Subjects

(A) Body-selective (blue) and motion-selective (yellow) activations in posterior ITS in six individual subjects, at $p < 0.001$.

(B) Body-selective (blue) and face-selective (yellow) activations in posterior fusiform gyrus in six individual subjects, at $p < 0.001$.

surrounding (and including) the peak voxel or as just the peak alone. One explanation of these results is that the body-selective, motion-selective, and face-selective neurons in these regions are all strongly activated by moving point-light figures (versus control), albeit to a different extent. This explanation would require a functional account of how neurons that are generally selective for visual motion, and other neurons selective for faces, contribute to biological motion perception. An alternative explanation, with substantially different functional implications, is that the biological motion activation in hMT+ and FFA is entirely due to the existence of body selectivity in these regions—perhaps in the form of body-selective neurons interspersed among face- or motion-selective neurons. On this account, motion selectivity and face selectivity are unrelated to biological motion selectivity.

Voxelwise Correlations

To distinguish between these explanations, we determined the voxel-by-voxel correlations between biological motion selectivity and selectivity for the localizer stimuli within each individually defined ROI (see Figure 3A for an overview). For example, we reasoned that if motion-selective area hMT+ processes biological motion, voxels within hMT+ that are relatively strongly motion selective (indicating that the voxel contains a relatively large number of motion-selective neurons) should also be relatively strongly selective for biological motion. In contrast, voxels that show weaker motion selectivity should also be less selective for biological motion. In other words, we would expect a positive voxelwise correlation between motion selectivity and biological motion selectivity in hMT+ if (1) the two conditions activate the same neurons and (2) the variation in selectivity across voxels is stable and reflects variations in the proportions of neurons exhibiting different kinds of selectivity. (For a similar argument, see Peelen and Downing, 2005c.) Likewise, the same logic can be applied to the posterior fusiform gyrus activations. If the face-selective neurons of the FFA are involved in processing biological motion, there should be a positive voxelwise correlation in this region between face selectivity and biological motion selectivity. In contrast, if biological motion activation in the FFA is explained by the presence of body-selective neurons within the voxels assigned to that ROI, we would expect a positive correlation only between body selectivity and biological motion selectivity in this region.

Note that in the above discussion we assume that each ROI consists of body-, face-, and motion-selective neurons, and then ask whether one of these populations is particularly engaged by biological motion. As we note in the Discussion, the same logic applies when we consider a less extreme scenario, in which a single population of neurons responds to varying degrees, and with different patterns across neurons, to the different stimulus types.

For each voxel in each ROI, on an individual subject basis, we calculated the biological motion selectivity (expressed by a t value for each voxel). Then, we correlated these t values with t values reflecting the motion and body selectivity in hMT+ and EBA, and body and face selectivity in FFA and FBA. The average correlations were then tested against zero, with subject as the random factor.

Voxel by voxel, biological motion selectivity was significantly correlated with body selectivity in all ROIs: left EBA ($r = 0.30$, $t_{17} = 5.4$, $p < 0.001$), right EBA ($r = 0.38$, $t_{17} = 5.8$, $p < 0.001$), left hMT+ ($r = 0.30$, $t_{17} = 3.6$, $p < 0.005$), right hMT+ ($r = 0.39$, $t_{17} = 5.0$, $p < 0.001$), FFA ($r = 0.31$, $t_{17} = 3.0$, $p < 0.01$), and FBA ($r = 0.14$, $t_{17} = 2.3$,

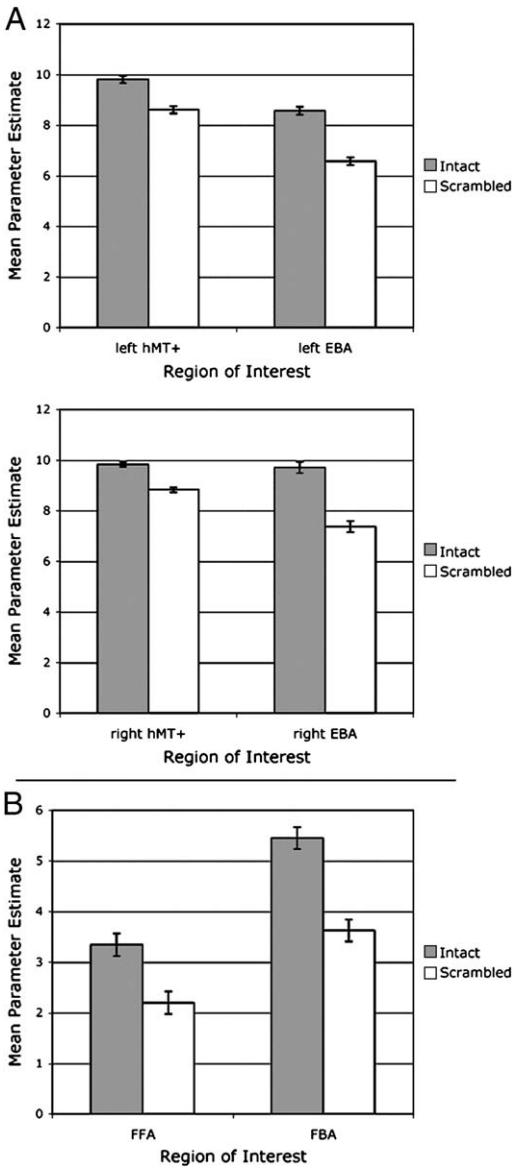

Figure 2. Biological Motion Activation in Regions of Interest

(A) Left hMT+ and left EBA (top panel), right hMT+ and right EBA (middle panel).

(B) FBA and FFA (bottom panel).

Error bars reflect within-subject SEM (Loftus and Masson, 1994).

$p < 0.05$). In contrast, biological motion selectivity did not correlate with motion selectivity in any of the pITS ROIs: left EBA ($r = -0.18$, $t_{17} = -2.0$, $p = 0.06$), right EBA ($r = 0.07$, $t_{17} = 0.7$, $p = 0.47$), left hMT+ ($r = 0.01$, $t_{17} = 0.1$, $p = 0.95$), and right hMT+ ($r = 0.00$, $t_{17} = 0.1$, $p = 0.92$). Nor was there a significant correlation with face selectivity in the pFG ROIs: FFA ($r = 0.13$, $t_{17} = 1.7$, $p = 0.10$), FBA ($r = 0.10$, $t_{17} = 0.8$, $p = 0.41$). Thus, in each region individually, biological motion selectivity was related to body selectivity but not motion or face selectivity.

To further generalize and verify these findings, we defined the union of EBA and hMT+ (which will be labeled pITS) and the union of FBA and FFA (which will be labeled pFG). This allows us to test for the general relationship between selectivities in these cortical "neighborhoods," without regard to whether a voxel is assigned to a particular labeled area. A further advantage of this analysis is that it controls for any differences in the main effect of biological motion that might exist between ROIs. That is, for example, it could be that the somewhat smaller biological motion effect in hMT+ (as compared to EBA) artificially suppresses the correlation between motion and biological motion.

Both left and right pITS were strongly body-, motion-, and biological motion selective (all p values < 0.001). Similarly, pFG was strongly body-, face-, and biological motion selective (all p values < 0.005). Within these larger ROIs, we again correlated the voxelwise patterns of biological motion selectivity with the patterns of body, motion, and face selectivity. Figure 3B gives the results of these analyses. Again, in all regions, biological motion selectivity correlated positively with body selectivity (left pITS: $r = 0.47$, $t_{17} = 5.7$, $p < 0.001$; right pITS: $r = 0.57$, $t_{17} = 7.4$, $p < 0.001$; pFG: $r = 0.38$, $t_{17} = 4.2$, $p < 0.001$) but not (or negatively) with motion selectivity (left pITS: $r = -0.34$, $t_{17} = -4.8$, $p < 0.001$; right pITS: $r = -0.31$, $t_{17} = -3.9$, $p < 0.005$) and face selectivity ($r = 0.05$, $t_{17} = 0.2$, $p = 0.83$). See Figures S1–S3 in the Supplemental Data avilable online for a graphical representation, in the form of scatterplots, of these results.

The negative correlations between motion selectivity and biological motion selectivity in pITS observed in the preceding analysis indicates that within the combined pITS ROI, EBA and hMT+ are to some degree discrete: voxels that are highly body- (and indeed biological motion-) selective tend to be nonresponsive to simple motion, and vice versa. Note that this relationship only becomes apparent due to the use of the present pattern analysis: as described above, even when the single most body- or motion-selective peak voxel from each region is considered, both ROIs show highly significant selectivity for biological motion.

Finally, to assess the independent predictive value of the voxelwise patterns of motion, body, and face selectivity to the patterns of biological motion selectivity in the three regions (left and right pITS, and pFG), we performed multiple regression analyses. For each subject and region, a regression model was tested with biological motion selectivity as the dependent variable and with body and motion selectivity (pITS) or body and face selectivity (pFG) as predictors. The obtained betas were accumulated across subjects and tested against zero. This analysis tests, for each area, whether body selectivity is a significant predictor of biological motion selectivity while simultaneously taking into account any shared variance with face or motion selectivity. Biological motion selectivity could be predicted by body selectivity in all regions (left pITS: $\beta = 0.45$, $t_{17} = 6.1$, $p < 0.001$; right pITS: $\beta = 0.54$, $t_{17} = 9.8$, $p < 0.001$; pFG: $\beta = 0.31$, $t_{17} = 3.4$, $p < 0.005$) but not by motion selectivity (left pITS: $\beta = -0.17$, $t_{17} = 2.0$, $p = 0.06$; right pITS: $\beta = -0.11$, $t_{17} = 1.4$, $p = 0.18$) or by face selectivity (pFG: $\beta = 0.13$, $t_{17} = 1.3$, $p = 0.22$).

Discussion

Our findings support three main conclusions, each of which we discuss in turn below. First, we resolve a longstanding ambiguity in studies of the neural basis of biological motion perception, by identifying and interpreting

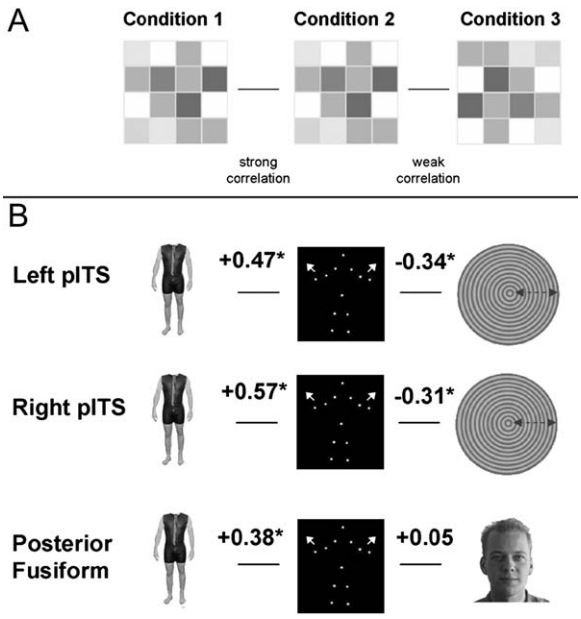

Figure 3. Voxelwise Correlations

(A) Schematic overview of the voxelwise correlation method: activations to different conditions were correlated voxel-by-voxel. Conditions 1 and 2 elicit a similar activation pattern and are therefore highly correlated. Conditions 2 and 3 have a dissimilar activation pattern and are not (or negatively) correlated.

(B) Voxelwise correlations between body, face, and motion selectivity, with biological motion selectivity in posterior ITS and posterior fusiform regions. Body selectivity correlated significantly with biological motion selectivity in all regions. Motion and face selectivity did not correlate, or correlated negatively, with biological motion selectivity.

the source of lateral ITS and posterior FG biological motion activations. Thus, this work significantly clarifies our emerging picture of how the human brain makes sense of the appearance and actions of other individuals. Second, we provide evidence for a highly selective, focal representation of the human body that closely overlaps, but is functionally separate from, the fusiform face area. This finding has important implications for interpreting the functional organization of this region. Finally, our results illustrate the power of combining a functional ROI approach with analyses of the response patterns within different ROIs. By localizing multiple, adjacent areas of interest and relating various types of selectivity on a voxel-by-voxel basis, we were able to draw conclusions that would be impossible with typical whole-brain group-average or individual-subject functional ROI analyses.

Biological Motion Perception

Numerous previous studies have supported the notion of a network of areas involved in the perception of other individuals. With respect to biological motion, the focus has been almost entirely on pSTS, to the exclusion of other posterior regions engaged by the same stimuli. Our results show that visual areas involved in analyzing the form of the human body (EBA, FBA) are selectively activated by sparse movement patterns that induce the percept of a person performing an action. In these regions, there was not only a global preference for point-light actors compared to scrambled controls, but also a strong voxel-by-voxel correlation between body selectivity and biological motion selectivity. Other areas (hMT+ and FFA) that substantially overlapped these regions also showed a significant selective activation to the biological motion displays. Strikingly, however, the voxelwise variation in response to these regions' preferred stimuli (simple motion and faces) bore no relationship to biological motion selectivity, while variation in body selectivity did. From these results we conclude that, in spite of the apparent biological motion selectivity of hMT+ and FFA, the motion- and face-selective neurons in these regions play no functional role in biological motion perception. Instead we attribute the biological motion response in these two general cortical areas to body-selective neurons in the EBA and FBA, respectively.

What do our results suggest about the pITS and pFG regions at the level of individual neurons? To use pITS as an example, one possibility is that the region contains two kinds of neurons, which are highly selective either for visual features of the human body or for visual motion. Alternatively, the distinction between motion- and body-selective neurons may be one more of degree than of kind. On this account, pITS neurons would respond to varying degrees to both visual motion and to visual aspects of the human body. Our results indicate that if this were the case, the distribution of these two kinds of selectivity would be largely independent. That is, variations in body selectivity from neuron to neuron would be unrelated to (and not predictable by) variations in motion selectivity—indicating functional independence of motion and body selectivity, even if these two functions are not divided in an absolute sense between two neural populations.

On either account, body and motion selectivity would have to be interleaved on a fairly fine scale (relative to the resolution of fMRI) to explain our findings of biological motion selectivity in hMT+ as well as EBA ROIs. The results of our pattern analyses, however, suggest consistent variation across voxels in the relative proportion of neural selectivity for bodies and for visual motion (e.g., Haynes and Rees, 2005; Kamitani and Tong, 2005).

What is the functional difference between the various posterior areas engaged by biological motion? Importantly, pSTS is not strongly selective for static bodies (e.g., Grossman and Blake, 2002), in contrast to the EBA and FBA. Although we cannot exclude the possibility that the response in pSTS to biological motion reflects form information derived from motion, we suggest instead that pSTS is activated specifically by particular motion patterns instead of the accompanying form information. This is consistent with a study by Beauchamp et al. (2002), who tested the neural response to the same bodies moving in either an articulated or unarticulated fashion. Significantly more activation was found in pSTS during articulated body movements, suggesting that the type of movement is a key predictor for pSTS activation. In contrast, areas EBA and FBA have been shown to selectively respond to static bodies even when they are depicted by very minimal visual cues, for instance a few lines forming a "stick figure" (Downing et al., 2001; Peelen and Downing, 2005a). In other words, the presence of the form of the body seems crucial for these areas, much more so than the presence of specific low-level visual features.

Taking these results together, we speculate that the EBA and FBA are largely "naive" about the patterns of changing posture that comprise biological actions, but instead simply respond to the presence of the form of the body. The pSTS, in contrast, integrates information over time and activates in response to movements that are biologically plausible. These suggestions are generally consistent with a recent computational model of biological motion perception, which proposes that pSTS integrates form information from a "ventral" pathway (which includes EBA) and motion information from a "dorsal" pathway (Giese and Poggio, 2003). Note, however, that this model does not take into account the recently discovered FBA; we turn next to a closer discussion of this region.

Body Selectivity and the Posterior Fusiform Gyrus

Body-selective responses in FBA, but not face-selective responses in overlapping area FFA, showed a strong relation to selectivity for biological motion. This finding is important because it shows that areas that are anatomically overlapping can be functionally dissociated. A recent study, using high-resolution (1.4 × 1.4 × 2.0 mm) fMRI, found that pFG body and face responses could also be partly distinguished spatially, in that in many subjects voxels could be identified that showed either body or face selectivity, but not both (Schwarzlose et al., 2005). Notably, areas of overlap remained between face- and body-selective regions. The present results suggest that body and face selectivity may be independent within the overlapping region and offers a method to test this possibility with high-resolution data.

The face selectivity of the posterior fusiform gyrus has been the matter of much recent debate (Kanwisher, 2000; Tarr and Gauthier, 2000). On one account, the FFA is not selective for faces as such, but is instead involved in a cognitive process that is usually most strongly employed by faces (Tarr and Gauthier, 2000). This cognitive process has been qualitatively described as subordinate discrimination of highly similar objects for which one has substantial expertise. This account of the FFA could potentially explain the strong body selectivity in this general region (Peelen and Downing, 2005a, Schwarzlose et al., 2005), as the perceptual processes involving bodies are in some ways similar to those involving faces (this is illustrated, for example, by the inversion effect found for both bodies and faces [Reed et al., 2003]). Importantly, the present evidence that body- and face-selective fusiform regions can be functionally dissociated refines our view of the properties of this region. We propose that it contains (at least) two functionally distinct domain-specific representations, overlapping at a relatively fine scale. These populations may share in common the property that they are suited to discriminating highly similar objects, which would be consistent with a domain-general account of the region as a whole.

Analysis of Multiple Overlapping Regions of Interest

As we have shown for two different broad brain regions (posterior inferior temporal sulcus and posterior fusiform gyrus), group-average coordinates of functionally quite different regions can be very close together. As a result, great caution should be taken in functionally labeling an activated region (e.g., "FFA") based on group-average coordinates, especially when the coordinates of this area come from a different group of subjects or a different study altogether.

One approach that researchers have taken to overcome this problem is to functionally localize ROIs in each subject, thus avoiding the problems that arise from intersubject averaging. However, our results show that this may not be sufficient to avoid false conclusions. Indeed, based simply on the overall amplitude differences that we found between intact and scrambled biological motion sequences (which were highly significant in each ROI individually, even when only peak voxels were considered), we might have falsely concluded that body-selective, motion-selective, and face-selective neurons are all involved in biological motion perception.

This highlights the importance of localizing not only regions of interest critical for one's hypothesis, but also other known nearby regions. When these regions overlap, as in the case of hMT+/EBA and FFA/FBA, this localization must be done within subjects, and ideally within sessions, to maximize the ability to distinguish functional regions. Finally, and critically, the pattern of responses to a contrast of interest, across the voxels that comprise each ROI, carries valuable information (Cox and Savoy, 2003; Haxby et al., 2001; Haynes and Rees, 2005; Kamitani and Tong, 2005). In the present study, analyzing these patterns allowed us to disentangle the sources of biological motion selectivity as observed at the aggregate ROI level. Because of the unique voxelwise relationship between body selectivity and biological motion selectivity, we can attribute the biological motion effects in hMT+ and FFA to the presence of body selectivity in the voxels of those ROIs.

Conclusion

To summarize, we have used a combination of multiple within-subject ROI definition and voxelwise pattern analyses to elucidate the functional network of brain regions involved in the analysis of biological motion. We believe this approach will prove useful both in further studies on the neural basis of "social vision" and more generally in studies of other regions where multiple functional areas occupy overlapping cortical territory.

Experimental Procedures

Subjects

Eighteen healthy adult volunteers were recruited from the University of Wales, Bangor community. Participants satisfied all requirements in volunteer screening and gave informed consent approved by the School of Psychology at the University of Wales, Bangor, and the North-West Wales Health Trust. Participation was compensated at £20 per session.

Design and Procedure

Each participant was scanned on three blocked-design fMRI experiments, in order to identify a priori functional regions of interest with respect to individual brain anatomy and to measure the response of these regions to biological motion stimuli. We localized the EBA and FBA with an experiment consisting of blocks of images of human faces, human bodies without heads, outdoor scenes, and handheld tools. The experiment consisted of 21 15 s blocks. Blocks 1, 6, 11, 16, and 21 were fixation-only baseline epochs. In each of the remaining blocks, 20 different images from one category were presented. Each

image appeared for 300 ms, followed by a blank screen for 450 ms. Twice during each block, the same image was presented two times in succession. Subjects were required to detect these repetitions and report them with a button press (1-back task). Image position was jittered slightly on alternate presentations, in order to disrupt attempts to perform the 1-back task based on low-level visual transients. Each participant was tested with two different order versions of the experiment, counterbalancing for the order of the blocks. In both versions, assignment of category to block was counterbalanced, so that the mean serial position in the scan of each condition was equated. Participants were tested with two (n = 14) or four (n = 4) runs of this experiment. Further details can be found elsewhere (Peelen and Downing, 2005a).

The blocked-design localiser for area hMT+ consisted of a pattern of low-contrast, concentric rings that either slowly oscillated inwards and outwards, or, in separate blocks, remained static (cf. Tootell et al., 1995). The experiment consisted of 21 15 s blocks. Blocks 1, 6, 11, 16, and 21 were fixation-only baseline epochs. In the remaining blocks, moving and static stimuli were alternated. The stimuli in this experiment were passively viewed. Participants were tested with one run of this experiment.

The biological motion experiment had a similar design to the hMT+ localiser, except that the blocks were 16 s long. In nonbaseline blocks, subjects passively viewed either 16 intact point-light animations of simple, whole-body actions (e.g., jumping or throwing) or scrambled controls of the same animations. Scrambled controls were made by keeping the component motions intact while randomizing the starting point of each dot. The animations were comprised of small white dots on a black background. Each animation lasted 667 ms, with a 333 ms blank interval before the next stimulus. Participants were tested with one (n = 13) or two (n = 5) runs of this experiment.

Data Acquisition

A 1.5T Philips MRI scanner with a SENSE parallel head coil was used. For functional imaging, a single-shot EPI sequence was used (T2* weighted, gradient echo sequence, TE = 50 ms, flip angle 90°). Scanning parameters were: TR = 3000 ms, 20–22 off-axial slices, voxel dimensions: 3.75 × 3.75 × 5 mm (n = 11), 3 × 3 × 4 mm (n = 6), or 2.5 × 2.5 × 2.5 mm (n = 1).

Preprocessing

Preprocessing and statistical analysis of MRI data were performed using BrainVoyager 4.9 (Brain Innovation, Maastricht, The Netherlands). Three dummy volumes were acquired before each scan in order to reduce possible effects of T1 saturation. Functional data were motion corrected, low-frequency drifts were removed with a temporal high-pass filter (0.006 Hz). No spatial smoothing was applied. Functional data were manually coregistered with 3D anatomical T1 scans (1 × 1 × 1.3 mm resolution). The 3D anatomical scans were transformed into Talairach space, and the parameters for this transformation were subsequently applied to the coregistered functional data, which were resampled to 1 × 1 × 1 mm voxels. The analyses were performed in Talairach space to allow comparison of ROI locations with previous (and future) studies. Because the normalization parameters were (for a given subject) identical for all conditions, normalization could not have systematically influenced the results (cf. Swallow et al., 2003).

Whole-Brain Analysis

A whole-brain, random-effects group average analysis was conducted on data from the biological motion experiment. Seventeen subjects were included in this analysis (one subject was excluded because we did not scan the whole brain in this subject). A contrast was performed at an uncorrected threshold of $p < 0.001$ to test for regions more active in the intact than the scrambled conditions. Only clusters >100 mm^3 are reported for this analysis.

ROI Analysis

For each participant, general linear models were created for each localiser experiment. One predictor (convolved with a standard model of the HRF) modeled each condition. Regressors of no interest were also included to account for differences in the mean MR signal across scans. Regressors were fit to the MR time series in each voxel, and the resulting parameter estimates were used to estimate the magnitude of response to each experimental condition.

In each participant, the localiser scans were used to define the EBA by contrasting the response to human bodies with that to the average of faces, tools, and scenes. The FBA was defined by contrasting bodies against tools, and the FFA was defined by contrasting faces against tools (Peelen and Downing, 2005a). (Note that in a recent study [Downing et al., 2005] we found that identification and characterization of these regions was little affected by the choice of baseline conditions.) We identified area hMT+ by contrasting the response to moving concentric rings with that to static rings. Analyses of the FBA and FFA were restricted to right hemisphere ROIs; on the basis of previous evidence these regions are weaker or nonexistent in the left hemisphere (Kanwisher et al., 1997; Peelen and Downing, 2005a).

For each ROI in each subject, the most significantly activated voxel was identified within a restricted part of cortex based on previously reported anatomical locations (EBA: Peelen and Downing, 2005b; hMT+: Dumoulin et al., 2000; FFA: Kanwisher et al., 1997; FBA: Peelen and Downing, 2005a). ROIs were defined as the set of contiguous voxels that were significantly activated (all $p < 0.001$ uncorrected) within a 9 × 9 × 9 mm cube surrounding (and including) the peak voxel. This procedure was adopted for four reasons: to ensure that regions were defined objectively, to ensure that they were segregated from nearby selective activations, to roughly equate the number of voxels included across different regions of interest, and to ensure that only the most selective voxels were included in the ROI. Within each ROI in each subject, a further general linear model was then applied, modeling the response of the voxels in the region (in aggregate) to the intact and scrambled biological motion conditions. The regression weights from this GLM provided the basis for the ROI amplitude results shown in Figure 2. A further analysis testing only the peak voxel of each ROI confirmed these results.

Correlation Analyses

For each ROI in each subject individually, we measured the voxel-by-voxel pattern of selectivity to key stimuli of interest. This was accomplished by extracting a t value for a given contrast at each voxel in the ROI. The t value provides a useful index of selectivity, because it combines in one number the magnitude of the difference between two conditions, relative to the within-condition variance. For all regions of interest, selectivity was measured for intact compared to scrambled point-light biological motion. For the pITS ROIs (hMT+ and EBA), motion selectivity was measured with moving versus static rings, and body selectivity with bodies versus the average of faces, tools, and scenes. For the pFG ROIs (FFA and FBA), face and body selectivity were measured with faces versus tools and with bodies versus tools, respectively.

These t values provided the raw materials for further analyses of the relationship between different kinds of selectivity within a given ROI. For the first type of analysis, we correlated, for each ROI, the pattern of selectivity for one contrast with the pattern for another. Thus, for example, we might correlate body selectivity and biological motion selectivity within the right EBA of a particular subject. These correlations were extracted for each subject individually, Fisher transformed, and the resulting mean correlation was tested statistically against zero.

For the second type of analysis, we computed similar correlations for ROIs defined by the union of the voxels of two individual ROIs (e.g., the union of right hMT+ and right EBA). This provides a test of the overall relationship between types of selectivity within a general region (e.g., posterior fusiform gyrus in the case of FFA/FBA; posterior ITS in the case of EBA/hMT+).

Finally, we used multiple regression to analyze how well biological motion selectivity could be predicted within a given ROI based on one kind of selectivity, while simultaneously taking into account another type of selectivity. For example, this analysis allowed us to ask to what extent biological motion selectivity could be predicted in EBA as a function of body selectivity, while accounting for any variance explained by motion selectivity. For each ROI in each subject, a linear model was fit with two kinds of selectivity as predictors and with biological motion selectivity as the to-be-predicted variable. An additional "flat" predictor was included to account for global differences in selectivity. The fit from each model resulted in a normalized

beta value for each of the two predictors of interest. These betas were collected from each subject individually and compared against zero with a t test.

Supplemental Data

The Supplemental Data for this article can be found online at http://www.neuron.org/cgi/content/full/49/6/815/DC1/.

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References

Allison, T., Puce, A., and McCarthy, G. (2000). Social perception from visual cues: role of the STS region. Trends Cogn. Sci. *4*, 267–278.

Beauchamp, M.S., Lee, K.E., Haxby, J.V., and Martin, A. (2002). Parallel visual motion processing streams for manipulable objects and human movements. Neuron *34*, 149–159.

Bonda, E., Petrides, M., Ostry, D., and Evans, A. (1996). Specific involvement of human parietal systems and the amygdala in the perception of biological motion. J. Neurosci. *16*, 3737–3744.

Cox, D.D., and Savoy, R.L. (2003). Functional magnetic resonance imaging (fMRI) "brain reading": detecting and classifying distributed patterns of fMRI activity in human visual cortex. Neuroimage *19*, 261–270.

Downing, P.E., Jiang, Y., Shuman, M., and Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. Science *293*, 2470–2473.

Downing, P.E., Chan, A.W.-Y., Peelen, M.V., Dodds, C.M., and Kanwisher, N. (2005). Domain specificity in visual cortex. Cereb. Cortex. in press. Published online December 7, 2005. 10.1093/cercor/bhj086.

Dumoulin, S.O., Bittar, R.G., Kabani, N.J., Baker, C.L., Le Goualher, G., Bruce Pike, G., and Evans, A.C. (2000). A new anatomical landmark for reliable identification of human area V5/MT: a quantitative analysis of sulcal patterning. Cereb. Cortex *10*, 454–463.

Giese, M.A., and Poggio, T. (2003). Neural mechanisms for the recognition of biological movements. Nat. Rev. Neurosci. *4*, 179–192.

Grèzes, J., Fonlupt, P., Bertenthal, B., Delon-Martin, C., Segebarth, C., and Decety, J. (2001). Does perception of biological motion rely on specific brain regions? Neuroimage *13*, 775–785.

Grossman, E.D., and Blake, R. (2001). Brain activity evoked by inverted and imagined biological motion. Vision Res. *41*, 1475–1482.

Grossman, E.D., and Blake, R. (2002). Brain areas active during visual perception of biological motion. Neuron *35*, 1167–1175.

Grossman, E., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., and Blake, R. (2000). Brain areas involved in perception of biological motion. J. Cogn. Neurosci. *12*, 711–720.

Grossman, E.D., Blake, R., and Kim, C.Y. (2004). Learning to see biological motion: brain activity parallels behavior. J. Cogn. Neurosci. *16*, 1669–1679.

Haxby, J.V., Gobbini, M.I., Furey, M.L., Ishai, A., Schouten, J.L., and Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. Science *293*, 2425–2430.

Haxby, J.V., Hoffman, E.A., and Gobbini, M.I. (2002). Human neural systems for face recognition and social communication. Biol. Psychiatry *51*, 59–67.

Haynes, J.D., and Rees, G. (2005). Predicting the stream of consciousness from activity in human visual cortex. Curr. Biol. *15*, 1301–1307.

Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. Percept. Psychophys. *14*, 201–211.

Kamitani, Y., and Tong, F. (2005). Decoding the visual and subjective contents of the human brain. Nat. Neurosci. *8*, 679–685.

Kanwisher, N. (2000). Domain specificity in face perception. Nat. Neurosci. *3*, 759–763.

Kanwisher, N., McDermott, J., and Chun, M.M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. J. Neurosci. *17*, 4302–4311.

Loftus, R., and Masson, E.J. (1994). Using confidence Intervals in within-subject designs. Psychon. Bull. Rev. *1*, 476–490.

Michels, L., Lappe, M., and Vaina, L.M. (2005). Visual areas involved in the perception of human movement from dynamic form analysis. Neuroreport *16*, 1037–1041.

Peelen, M.V., and Downing, P.E. (2005a). Selectivity for the human body in the fusiform gyrus. J. Neurophysiol. *93*, 603–608.

Peelen, M.V., and Downing, P.E. (2005b). Within-subject reproducibility of category-specific visual activation with functional MRI. Hum. Brain Mapp. *25*, 402–408.

Peelen, M.V., and Downing, P.E. (2005c). Is the extrastriate body area involved in motor actions? Nat. Neurosci. *8*, 125.

Pelphrey, K.A., Morris, J.P., Michelich, C.R., Allison, T., and McCarthy, G. (2005). Functional anatomy of biological motion perception in posterior temporal cortex: an fMRI study of eye, mouth and hand movements. Cereb. Cortex *15*, 1866–1876.

Peuskens, H., Vanrie, J., Verfaillie, K., and Orban, G.A. (2005). Specificity of regions processing biological motion. Eur. J. Neurosci. *21*, 2864–2875.

Reed, C.L., Stone, V.E., Bozova, S., and Tanaka, J. (2003). The body-inversion effect. Psychol. Sci. *14*, 302–308.

Santi, A., Servos, P., Vatikiotis-Bateson, E., Kuratate, T., and Munhall, K. (2003). Perceiving biological motion: dissociating visible speech from walking. J. Cogn. Neurosci. *15*, 800–809.

Saygin, A.P., Wilson, S.M., Hagler, D.J., Bates, E., and Sereno, M.I. (2004). Point-light biological motion perception activates human premotor cortex. J. Neurosci. *24*, 6181–6188.

Schwarzlose, R., Baker, C., and Kanwisher, N. (2005). Separate face and body selectivity on the fusiform gyrus. J. Neurosci. *25*, 11055–11059.

Swallow, K.M., Braver, T.S., Snyder, A.Z., Speer, N.K., and Zacks, J.M. (2003). Reliability of functional localization using fMRI. Neuroimage *20*, 1561–1577.

Talairach, J., and Tournoux, P. (1988). Co-Planar Stereotaxic Atlas of the Human Brain (Stuttgart: Thieme).

Tarr, M.J., and Gauthier, I. (2000). FFA: a flexible fusiform area for subordinate-level visual processing automatized by expertise. Nat. Neurosci. *3*, 764–769.

Tootell, R.B., Reppas, J.B., Kwong, K.K., Malach, R., Born, R.T., Brady, T.J., Rosen, B.R., and Belliveau, J.W. (1995). Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. J. Neurosci. *15*, 3215–3230.

Vaina, L.M., Solomon, J., Chowdhury, S., Sinha, P., and Belliveau, J.W. (2001). Functional neuroanatomy of biological motion perception in humans. Proc. Natl. Acad. Sci. USA *98*, 11656–11661.